Skeletal correlates of quadrupedalism and climbing in the anthropoid forelimb: Implications for inferring locomotion in Miocene catarrhines

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Abstract: Several well-known Miocene catarrhines, including Proconsul heseloni, have been inferred to combine quadrupedal walking in an arboreal substrate with a significant amount of climbing during locomotion. The degree to which some of these species were adapted to perform these behaviors is not fully understood due to the mosaic of 'ape-like' and 'monkey-like' traits identified in the forelimb. Given these unique combinations of forelimb features in the fossils, we report on forelimb traits that should be emphasized when investigating skeletal adaptation to quadrupedalism (defined in this manuscript as symmetrical gait movement on horizontal supports, excluding knuckle-walking) and climbing (including both vertical climbing and clambering). We investigate the correspondence between: 1) quadrupedalism and two well-known forelimb traits, humeral torsion and olecranon process length, and 2) climbing and phalangeal curvature. We also test the degree of phylogenetic signal in these relationships using phylogenetic generalized least-squares and branch length transformation methods in order to determine the models of best-fit. We present models that can be used to predict proportions of quadrupedalism and climbing in extant and extinct anthropoid taxa. Each trait–behavior correlation is significant and characterized by an absence of phylogenetic signal. Thus, we employ models assuming a star phylogeny to predict locomotor proportions. The climbing model based on phalangeal curvature and a proxy for size provides the most accurate predictions of behavior across anthropoids. The two quadrupedalism models are less accurate, but distinguish highly quadrupedal species from those that are not. Predictive equations based on these traits support the inference that P. heseloni performed a high proportion of quadrupedalism with a significant climbing component. The degree of phalangeal curvature measured in Pliopithecus vindobonensis predicts that this Miocene catarrhine species performed a proportion of climbing similar to Proconsul, while humeral torsion and olecranon process length provide conflicting inferences of quadrupedal locomotion in this species.

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Skeletal correlates of quadrupedalism and climbing in the anthropoid forelimb: Implications for inferring locomotion in Miocene catarrhines

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Key words: *Pliopithecus vindobonensis*; *Proconsul heseloni*; Humeral torsion; Included angle

Abstract

Several well-known Miocene catarrhines, including *Proconsul heseloni*, have been inferred to combine quadrupedal walking in an arboreal substrate with a significant amount of climbing during locomotion. The degree to which some of these species were adapted to perform these behaviors is not fully understood due to the mosaic of "apelike" and "monkeylike" traits identified in the forelimb. Given these unique combinations of forelimb features in the fossils, we report on forelimb traits that should be emphasized when investigating skeletal adaptation to quadrupedalism (defined in this manuscript as symmetrical gait movement on horizontal supports excluding knuckle-walking) and climbing (including both vertical climbing and clambering). We investigate the correspondence between: 1) quadrupedalism and two well-known forelimb traits, humeral torsion and olecranon process length, and 2) climbing and phalangeal curvature. We also test the degree of phylogenetic signal in these relationships using phylogenetic generalized least-squares and branch length transformation methods in order to determine the models of best-fit. We present models that can be used to predict proportions of quadrupedalism and climbing in extant and extinct anthropoid taxa. Each trait-behavior correlation is significant and characterized by an absence of phylogenetic signal. Thus, we employ models assuming a star phylogeny to predict locomotor proportions. The climbing model based on phalangeal curvature and a proxy for size provides the most accurate predictions of behavior across anthropoids. The two quadrupedalism models are less accurate, but distinguish highly quadrupedal species from those that are not. Predictive equations based on these traits support the inference that *Proconsul heseloni* performed a high proportion of quadrupedalism with a significant climbing component. The degree of phalangeal curvature

measured in *Pliopithecus vindobonensis* predicts that this Miocene catarrhine species performed a proportion of climbing similar to *Proconsul*, while humeral torsion and olecranon process length provide conflicting inferences of quadrupedal locomotion in this species.

Introduction

Forelimb skeletal elements are relatively common and well preserved in the catarrhine fossil record. The extent to which these postcranial elements act as reliable indicators of locomotor behavior in extinct catarrhines, however, is uncertain. Since the limb morphology of an organism represents a compromise of phylogeny, developmental constraints, and selective pressures, it is important to tease apart these different influences and examine the degree to which limb features indicate current locomotor adaptation or reflect phylogenetic heritage or development in order to present a refined assessment of locomotor behavior based on fossilized remains. Recent advances in comparative methods make it possible to test the relative correspondence between skeletal traits and locomotor behavior across a wide range of species while taking into account potential phylogenetic signal (Spoor et al., 2007). Using these methods, one can build predictive models that allow inferences about individual behaviors that make up an extinct taxon's locomotor profile based on the most reliable indicators of each behavior (e.g., Silcox et al., 2009).

Symmetrical gait quadrupedalism on horizontal substrates (similar to that observed in cercopithecoids) and climbing with powerful pollical grasping have been suggested to make up the majority of the locomotor repertoire of several Miocene catarrhines, such as *Proconsul*, *Afropithecus*, *Equatorius*, and *Sivapithecus* (Begun et al., 1994; Rose, 1994; Ward, 1998; Madar et al., 2002; Sherwood et al., 2002; Dunsworth, 2006). Quadrupedalism has also been inferred to play an important role in another well-represented Miocene catarrhine, *Pliopithecus vindobonensis* (Zapfe, 1958, 1960; Rose, 1994). Researchers have suggested, however, that other behaviors, including climbing, suspension, and leaping, contributed more to the

Pliopithecus locomotor repertoire compared to that of *Proconsul* (Simons and Fleagle, 1973; Szalay and Delson, 1979; Fleagle, 1983; Rose, 1994; Scherf, 2007). Predictive models for quadrupedalism and climbing can be used to critically test these inferences.

In the current study, we re-examine aspects of the locomotor behavior of *Proconsul heseloni* and *Pliopithecus vindobonensis*. The *Proconsul heseloni* type specimen, KNM-RU 2036, is a partial skull and postcranial skeleton that was found at site R114, Rusinga Island, Kenya (Walker et al., 1993). In terms of the forelimb, KNM-RU 2036 preserves complete or fragmentary remains of the scapula, humerus, radius, ulna, carpals, metacarpals, and phalanges. The consensus is that *Proconsul* was an above branch arboreal quadruped capable of powerful cheiridial grasping during climbing (Corrucini et al., 1975; Morbeck, 1975; Rose, 1983, 1993b; Walker and Pickford, 1983; Begun et al., 1994; Ward, 1998; Dunsworth, 2006). This is based on a combination of traits observed in several *Proconsul* species in which some features are characteristic of arboreal quadrupedal cercopithecoids and platyrrhines, whereas others are characteristic of hominoids that engage in vertical climbing (Rose, 1993b). This mosaic is identified throughout the forelimb. Proximally, the humeral shaft is characterized by a broad and shallow bicipital groove and flat deltoid plane with well-developed deltopectoral and deltotriceps crests as observed in extant arboreal cercopithecoids, whereas the shape of the zona conoidea and capitulum more closely resembles extant hominoids (Napier and Davis, 1959; Rose, 1993b; Walker, 1997; Ward, 1998). Distally, the proximal joint surface of the first metacarpal is sellar, allowing greater ranges of abduction/adduction and enhanced grasping ability used during climbing, whereas overall phalangeal dimensions most closely resemble above branch arboreal quadrupeds (Rafferty, 1990; Rose 1992; Begun et al., 1994; Ward, 1998).

Pliopithecus vindobonensis is a well-known central European catarrhine dating to the middle and late Miocene. The skeletal remains of several individuals were recovered from a fissure-fill near Neudorf an der March (Devínska Nová Ves, Slovakia). Forelimb specimens representing this species include a complete humerus, two complete ulnae, two complete radii, complete metacarpals, and several complete proximal phalanges. There have been various interpretations of the locomotor behavior of *Pliopithecus vindobonensis* over the past fifty years. Zapfe (1958, 1960) interpreted the *Pliopithecus vindobonensis* postcranium as representing a locomotor generalist that was not restricted to an arboreal environment and most likely moved quadrupedally on the ground as well. Szalay and Delson (1979) proposed that *Pliopithecus vindobonensis* engaged in a wide range of arboreal locomotor activities including suspension, leaping, climbing, and running. Later analyses of the overall postcranium (Fleagle, 1983) and pedal skeleton (Langdon, 1986) suggested that this species did not perform a significant amount of quadrupedalism and leaping and was mainly engaged in suspensory and climbing behavior (similar to *Ateles*). Rose (1994) reported that the *Pliopithecus* postcranium contains extensive evidence for quadrupedalism along with more evidence for climbing and suspensory behavior than what is observed in *Proconsul*. Forelimb evidence for arboreal quadrupedalism includes large greater and lesser tuberosities separated by a wide bicipital groove on the proximal humerus, a relatively flat and distally facing zona conoidea that articulates with a well developed rim on the lateral aspect of the radial head, and carpals that are similar in morphology to quadrupedal anthropoids (Corrucini et al. 1975; Fleagle, 1983; Rose, 1988, 1994). These traits stabilize the elbow and wrist during loading associated with quadrupedal locomotion. Forelimb characters interpreted as indicating climbing and suspension include the shape of the humeral shaft and degree of phalangeal curvature (Zapfe 1958; Begun, 1988; Rose, 1994). Many of the

suspensory traits identified in the *Pliopithecus* postcranium are located in the hind limb, including aspects of the proximal femur, knee, and ankle joint (Zapfe 1960; Fleagle, 1983; Langdon, 1986; Rose, 1994). Based on a recent examination of the trabecular architecture in the proximal femur, Scherf (2007) concluded that *Pliopithecus vindobonensis* was a locomotor generalist that occasionally performed quadrupedal locomotion, leading to relatively thick trabeculae in the superior aspect of the femoral head.

Humeral torsion refers to the orientation of the humeral head relative to the distal axis of the bone and has been extensively studied in primate skeletons (Martin, 1933; Inman et al., 1944; Evans and Krahl, 1945; Napier and Davis, 1959; Sarmiento, 1985; Larson, 1988, 1996, 2006). In quadrupedal monkeys, the humeral head faces posteriorly to articulate with a ventrally oriented glenoid fossa, whereas the hominoid humeral head is medially oriented to articulate with a laterally oriented glenoid cavity (Larson, 1996). Scapular position has been shown to differ across anthropoid clades, with hominoids having the most dorsally positioned scapula, suspensory platyrrhines having a more laterally positioned scapula, and highly terrestrial cercopithecoids being characterized by the most laterally positioned scapula (Erikson, 1963; Sarmiento, 1985; Chan, 2007). In addition to scapular position, studies of captive versus wild-shot orangutans (Sarmiento, 1985) and of human athletes in the sports medicine literature (Pieper, 1998; Osbahr et al., 2002) have suggested that humeral torsion is responsive to the mechanical activity performed over an individual's lifetime.

The olecranon process is the insertion site for the triceps brachii, a muscle that is responsible for elbow extension. Much work has been done investigating the length and orientation of the olecranon process in relation to the moment arm of the triceps brachii (Oxnard, 1963; Jolly, 1967, 1972; Knussmann, 1967; Ciochon, 1986, 1993; Harrison, 1989; Drapeau, 2004). The

olecranon process is relatively longer in highly quadrupedal cercopithecoids and platyrrhines compared to suspensory anthropoids (Jolly, 1967, 1972; Harrison, 1989; Rose, 1993a; Drapeau, 2004). Contrasting results have been reported for relative length differences between arboreal and terrestrial quadrupeds (Rodman, 1979; Ciochon, 1993; Drapeau, 2004). An elongated olecranon process in arboreal quadrupeds has been related to increasing the power of the triceps brachii muscle during the bent-elbow posture performed during arboreal quadrupedalism, whereas the relatively shorter olecranon process in highly terrestrial quadrupeds has been explained as allowing fuller elbow extension when moving on the ground (Rodman 1979). However, Drapeau (2004) found no difference in olecranon process length between highly arboreal and terrestrial quadrupeds when size was taken into account.

Due to its potential as a reliable indicator of locomotor behavior, phalangeal curvature has been studied through biomechanical, ontogenetic, and comparative analyses to uncover the nature of the functional relationshisps (Preuschoft, 1973; Stern and Susman, 1983; Susman et al., 1984; Rose, 1986; Stern et al., 1995; Jungers et al., 1997; Richmond, 1998, 2007; Deane et al., 2005; Deane and Begun, 2008). Phalangeal curvature has been measured most often using the included angle of curvature, which can be calculated from three linear measurements (see Material and Methods section; Susman et al., 1984; Rose, 1986; Stern et al., 1995; Jungers et al., 1997; Richmond, 1998). Deane et al. (2005) introduced a new method using high-resolution polynomial curve fitting that can measure curvature on fragmentary fossil specimens. A high degree of phalangeal curvature appears to signal suspensory and climbing behavior across clades, including hominoids and atelids (Stern et al., 1995; Deane et al., 2005), whereas terrestrial quadrupedal primates have phalanges with relatively low degrees of curvature (Jungers et al., 1997). Richmond (1998, 2007) demonstrated that high levels of curvature help alleviate

the strains on the phalanx during suspensory and climbing behaviors, and the presence of this character state correlates with intraspecific changes in locomotor behavior in hominoids during ontogeny.

Building on this previous work, we test the ability of phalangeal curvature to predict proportions of climbing and the ability of humeral torsion and olecranon process length to predict proportions of quardupedalism performed by anthropoid species for which locomotion has been observed in natural settings. When building predictive models of this kind based on a range of taxa, it is essential to test whether one should incorporate inferred phylogenetic relationships and estimated branch lengths in order to take into account covariation between closely related species. Thus, the present study employs phylogenetic generalized least-squares (pGLS) to investigate potential phylogenetic structuring of the data (Rohlf, 2006; Walker et al., 2008).

In this paper, we investigate the degree of phylogenetic signal in the correlation between each forelimb skeletal trait and locomotor category. Using pGLS with branch length transformation methods, we present the regression model of best-fit that should be used to examine the relationship between forelimb morphology and behavior. Next, we investigate the correspondence between each skeletal character and behavior using regression analysis. We also analyze the relative accuracy of quadrupedalism and climbing predictions based on each forelimb trait using extant test taxa for which locomotor behavior has been observed in natural settings. Based on these results, we employ the most accurate predictive models to infer the degree to which quadrupedalism and climbing contributed to the locomotor repertoires of *Proconsul heseloni* and *Pliopithecus vindobonensis*.

Material and methods

Skeletal samples

Measurements were taken on the humerus, ulna, and third proximal phalanx of the manus in extant taxa. Identification of the third manual phalanx was based on previously published methods as well as observations made during data collection (Begun, 1993; Richmond, 1998). The left bone was chosen for measurement unless unavailable, in which case the right was used. The target sample size for each taxon was 20 individuals (see Tables 1 and 2 for measurements and sample sizes). We measured an equal number of males and females for each species whenever possible. We only included female *Pongo pygmaeus* and male *Macaca fascicularis* in regression analyses of locomotion since published proportion data are based on a single sex.

TABLE 1 ABOUT HERE

The modern human skeletal sample includes 20 adult individuals from the Hamann-Todd Collection located at the Cleveland Museum of Natural History. We only collected nonhuman primate data on adult, non-pathological, wild-shot individuals from American Museum of Natural History (New York, NY), Harvard Museum of Comparative Zoology (Cambridge, MA), National Museum of Natural History (Washington, DC), Field Museum of Natural History (Chicago, IL), Natural History Museum (London, England), Powell-Cotton Museum (Birchington, England), Anthropologisches Institut und Museum (Zurich, Switzerland), Royal Museum of Central Africa (Tervuren, Belgium), Humboldt Museum für Naturkunde (Berlin,

Germany), and the National Museums of Kenya (Nairobi, Kenya). We selected species to measure based on data available for locomotor proportions in natural settings. Measurements were also taken on the original *Proconsul heseloni* KNM-RU 2036 partial skeleton at the National Museums of Kenya in Nairobi and on computed tomography (CT) scans of *Pliopithecus vindobonensis* forelimb bones located at the Naturhistorische Museum Basel and Naturhistorische Museum Wien.

TABLE 2 ABOUT HERE

Locomotion data

Locomotor data included in this study were based on published observations of adult individuals in wild populations during both feeding and traveling behavior. Proportions of locomotion during feeding and traveling were weighted based on the number of observations made by researchers in the field. In addition to noted variation in locomotion due to the age and sex of observed individuals, observational data regarding locomotion can vary within and between taxa based on differences in sampling methods, the categories into which different behaviors are grouped, and differences in the seasonal and environmental context in which observed populations are found (Doran, 1992, 1993; Doran and Hunt, 1994; Dagosto, 1995; Gebo and Chapman, 1995a, 1995b; McGraw, 1996; Dagosto and Yamashita, 1998). Thus, it is important to take into account all of the locomotor data available for each species in order to attempt to control for intraspecific variation in locomotor behavior. In this study, reported locomotor proportion data from multiple studies of adult individuals from a particular species

were averaged in an attempt to control for variation in locomotor behavior caused by differences in the habitat structure and the season in which data were collected (Table 3).

TABLE 3 ABOUT HERE

Locomotor proportions used in this paper come from published field studies on a wide range of primates. Thus, proportions based on both bout sampling and instantaneous sampling techniques are employed in the following regression analysis. One must use these data with caution since bout sampling and instantaneous sampling are not necessarily directly comparable (as described in detail by Dagosto and Gebo [1998]). In many cases, however, proportions of quadrupedalism or climbing behavior reported for the species examined are corroborated by more than one field study.

Another source of variation across published locomotor studies is the difference in choice of locomotor categories used by researchers to describe the behavior of focal animals. Primates perform a wide range of locomotor behaviors, yet many studies of primate locomotion lump all observed behaviors into four or five categories. Of particular note, vertical climbing (ascent up a support greater than or equal to 45°) and pronograde clambering (quadrupedal progression lacking a regular gait on small, angled supports) have often been grouped together into the general category of climbing (as discussed in Hunt et al. [1996]). Due to this method of categorization, we use a climbing category that includes both vertical climbing and pronograde clambering in order to include all taxa measured. Quadrupedalism includes symmetrical gait locomotion on top of supports angled at less than 45°. We do not include proportions of knuckle-walking and fist-walking in this category due to differences in limb kinematics between

these specialized behaviors and the types of quadrupedalism performed in cercopithecoids and platyrrhines. Thus, the models presented in this manuscript do not take into account all of the ways in which primates have adapted to quadrupedal locomotion and they should not be employed to predict proportions of knuckle-walking or fistwalking behavior. Mean locomotor proportions for quadrupedalism and climbing with a list of references for individual field studies are presented in Table 3.

Phylogenetic data

The inferred phylogenetic tree and branch lengths are based on molecular data since they provide an independent method for inferring phylogenetic relationships that does not involve the morphological traits being tested in this study. The divergence dates we use in this study come from several sources since most studies focus narrowly on subunits of the anthropoid clade (Fig. 1). Given that these studies employ different methods, however, there is the possibility of incompatibilty in the tree divergence dates. The divergence dates used in this study are consistent with those reported by Fabre et al. (2009) based on molecular supermatrix analyses.

FIG. 1 ABOUT HERE

Size data

Since regression analyses are performed on mean locomotor proportions and skeletal trait values for each species in this study, we use mean species size surrogate data to incorporate size

into multiple regression analysis. Table 2 presents data on the size surrogates used for the ulna and phalanx. A size surrogate was not included for the humerus since humeral torison alone was found to be the best predictor of quadrupedal locomotion. Each size surrogate has a strong and isometric correpondence with published mean species body mass values (from Smith and Jungers [1997]). We use the maximum dorsopalmar length of the phalangeal midshaft and the geometric mean of five proximal ulnar measurements described by Drapeau (2004) as size proxies.

Skeletal data collection

Humeral torsion, olecranon process length, and included angle of curvature of the third proximal phalanx were calculated from 3D coordinate data. Three-dimensional coordinates were collected with a Microscribe digitizer for all extant taxa and *Proconsul heseloni*. Comparable 3D coordinate landmarks were collected on CT scans of *Pliopithecus vindobonensis* bones using Landmark Editor (Wiley, 2006). We calculated the humeral torsion angle from four landmark points with x,y,z coordinates. These landmarks include the distal most point on edge of articular surface of humeral head bisecting the articular surface (landmark 1), a point on the proximal border of the head along the axis bisecting the articular surface (landmark 2), the most distal point on the medial trochlear keel (landmark 3), and the most distal point on the capitulum (landmark 4; Fig. 2). The vector between landmarks 1 and 2 represents the proximal transverse axis and the vector between landmarks 3 and 4 represents the distal transverse axis. In order to measure the humeral torsion angle, several steps must be taken. First, midpoints of the proximal and distal vectors are calculated. Next, the main longitudinal axis is defined as the axis between

these proximal and distal midpoints. By calculating the vector cross products between the the longitudinal axis and the proximal and distal transverse axes, respectively, parallel proximal and distal vectors are created that preserve the torsion angle between the proximal and distal axes. These parallel proximal and distal vectors are then normalized to produce two unit vectors. Finally, it is necessary to take the inverse cosine of the scalar product of the two unit vectors to calculate the torsion angle in radians. The value in radians can be easily converted to degrees [angle * (180/pi)]. The torsion angle is comparable to that reported in Larson (1996).

FIG. 2 ABOUT HERE

Olecranon process length (OL) is based on the measurement taken by Drapeau (2004), in which OL is measured from the approximate center of rotation of the ulna in flexion and extension movements. We measured olecranon process length as the distance between landmark 6 and landmark 9. Data extraction was performed in R version 2.10.1 (R Development Core Team, 2010). Direct interlandmark distances (d) were extracted using Pythagorean formula for three-dimensions (e.g., Young, 2004):

$$d = \mathrm{sqrt}((x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2)$$

Three extracted measurements are used to calculate included angle of curvature, including the length between the midpoint of the proximal articular surface (landmark 15) and the midpoint of the distal articular surface (landmark 18), the length between the dorsal midshaft (landmark 16) and palmar midshaft (landmark 17), and the length from the dorsal extent of the midshaft (landmark 16) to the line connecting the midpoints of proximal and distal articular surfaces (landmark 15 and landmark 18; Stern et al., 1995). Landmarks for these measurements are found

in Figure 2. Included angle values calculated from these measurements are comparable to those reported by Stern et al. (1995).

The five measurements comprising the ulna skeletal size surrogate include proximodistal height of the trochlear notch (measured with a Microscribe between landmark 5 and landmark 7), maximum depth of the trochlea (measured with a Microscribe between landmark 6 and landmark 8), proximodistal diameter of the radial notch (measured with a Microscribe between landmark 11 and landmark 12), anteroposterior length of the coronoid process (measured with calipers between landmark 5 and landmark 10), and anteroposterior diameter at the midshaft (measured with a Microscribe between landmark 13 and landmark 14; Drapeau, 2004). Landmarks for these measurements are shown in Figure 2. The proximal phalanx size surrogate, anteroposterior diameter of the midshaft (between landmark 16 and landmark 17), is measured with the Microscribe digitizer.

Data analysis

Proportion data characterizing quadrupedalism and climbing are separately regressed against the size surrogates and individual skeletal traits in 17 extant anthropoid species to investigate the correspondence between locomotion and forelimb morphology. During preliminary analyses, we found that models that employed humeral torsion without a size surrogate outperformed regressions that contained both humeral torsion and a size surrogate as independent variables. In contrast, we found that included angle of curvature models that contained a size proxy had a much stronger and more significant relationship between curvature and proportions of climbing than models that did not take size into account. Thus, the humeral torsion models presented in

this manuscript do not have a size proxy as an additional independent variable whereas curvature models do take size into account.

The locomotor variables are logistically transformed in order to linearize the data and allow them to be used as dependent variables in least-squares regression analysis ($\log[y/[1 - y]]$ where y is a proportion between zero and one; Warton and Hui, 2011). As suggested by Warton and Hui (2011), since proportions equal to zero and one transform to undefined values, a small value (0.01) was added to each species' proportion of quadrupedalism and climbing so that *Homo sapiens* and *Hylobates lar* could be added to the analysis. This small value was not added to the proportion of *Papio anubis* quadrupedalism since the value is 0.99. Each skeletal variable is $\log_{10}$ transformed and employed as an independent variable in regression.

We employed phylogenetic generalized least-squares regression in this analysis. Generalized least-squares models that take into account phylogeny can be based on different underlying models of evolutionary change. Two of the main models used in comparative methods include Brownian motion (BM) and Orstein-Uhlenbeck (OU). Brownian motion refers stochastic evolutionary change occurring at a constant rate (Martins and Garland, 1991; Garland, 1992; Blomberg et al., 2003; O'Neill and Dobson, 2008). This model assumes that the extent of trait variation between two species is based solely on the amount of evolutionary time since they diverged (O'Neill and Dobson, 2008). The Orstein-Uhlenbeck model is basically a Brownian motion model with an additional parameter that assumes stabilizing selection (Martins et al., 2002; Blomberg et al. 2003; O'Neill and Dobson, 2008). The OU model limits random evolution by a force proportional to the difference between the character value and a fixed optimum (Garland et al., 1993; Martins et al., 2002; Blomberg et al., 2003; O'Neill and Dobson, 2008).

Comparative methods, such as pGLS, assume that the degree of phylogenetic structuring present in the data fits the underlying evolutionary model employed. However, the degree of covariation based on phylogeny varies from one trait to the next. Thus, it is important to estimate the degree of phylogenetic signal in the correlation of skeletal traits and locomotor behaviors to ensure that the relationship is investigated under the proper regression model. If the chosen model is incorrect, analyses can lead to higher Type I error rates and invalid results (Freckleton et al., 2002; Rohlf, 2006).

In order to determine the model of best-fit for each behavior and prediction, we tested four different models including ordinary least-squares (OLS), phylogenetic generalized least-squares (pGLS) under Brownian motion, the pGLS model based on Pagel's λ transformation, and the pGLS model based on the *d* parameter (assuming an Ornstein-Uhlenbeck model of evolution; Pagel, 1999; Freckleton et al., 2002; Martins et al., 2002; O'Neill and Dobson, 2008). Phylogenetic generalized least-squares regression employs a variance-covariance matrix in which the diagonals represent the estimated branch lengths from the root of the tree to each species, and the off-diagonals represent the branch length shared by pairs of species from the root to their last common ancestor (Rohlf, 2006; Spoor et al., 2007; Walker et al., 2008). This variance-covariance matrix is used in a weighted least-squares regression that incorporates covariance related to phylogeny (Rohlf, 2006; Walker et al., 2008). All pGLS regressions are run in REGRESSIONv2.M in Matlab (available from T. Garland, University of California Riverside, Riverside, CA).

These four regression models (characterized by different evolutionary assumptions) are tested in order to examine potential covariation among closely related taxa (i.e., phylogenetic signal) in trait-behavior correlations and choose the best model with which to make predictions.

The Akaike information criterion for small sample sizes (AIC_c) was used to judge the model of best-fit. A lower AIC_c indicates a better fit for the model. These methods are similar to those employed by Spoor et al. (2007) when investigating the relationship between locomotor agility and semicircular canal morphology. The predictive accuracy of the models of best-fit are then tested for quadrupedal and climbing locomotion.

We first investigated the utility of these prediction models with cross-validation. This approach randomly divides one's data into groups of training sets (data on which models are based) and test sets (data on which predictive accuracy is tested; Maindonald and Braun, 2007). We employed each of the 17 species as a test case. We measured overall mean squared error in behavioral predictions based on each model. This analysis was performed in R version 2.10.1 (R Development Core Team, 2010).

We also used each model to predict proportions of quadrupedalism and climbing performed by two extant test anthropoids not included in the original analysis and for which locomotor profiles have been observed in natural settings. These taxa include two arboreal quadrupeds, *Cebus apella* and *Cercopithecus ascanius*. Point predictions and 95% confidence intervals are calculated for these test taxa and compared to observed proportions of locomotion in these species. In addition, predictions of quadrupedalism in these two test taxa were compared to those of a highly suspensory hominoid, *Pongo abelii*, which is characterized by minimal amounts of quadrupedal locomotor behavior. A similar comparison was not performed for proportions of climbing since we did not have the three measurements necessary to calculate included angle of curvature in *Pongo abelii* phalanges. Finally, regression models for climbing and quadrupedalism are applied to the *Proconsul heseloni* and *Pliopithecus vindobonensis* forelimbs.

Results

Table 4 presents a comparison of the Akaike information criterion for small sample sizes (AIC_c) between a conventional regression model (based on a star phylogeny), phylogenetic generalized least-squares (pGLS) based on Brownian motion, and pGLS based on Pagel's lambda and OU transformations. In all three cases, the AIC_c is lowest for conventional least-squares analyses. In addition, Pagel's lambda and OU transformations estimate an absence of phylogenetic signal in each correlation and provide regression coefficients that are identical to ordinary least-squares. Thus, humeral torsion and olecranon process length (when size is taken into account) have strong functional relationships with quadrupedalism across anthropoids that can be investigated without information on phylogenetic structuring. When size is taken into account, curvature of the third proximal phalanx has a high correspondence with climbing behavior that is also characterized by an absence of phylogenetic signal.

TABLE 4 ABOUT HERE

Table 5 describes the regression coefficients for the models of best-fit (ordinary least-squares in each case). Humeral torsion decreases as the proportion of quadrupedalism increases. Highly quadrupedal anthropoids have a more posteriorly positioned humeral head compared to suspensory hominoids and atelids and highly terrestrial hominoids. Olecranon process length increases with higher proportions of quadrupedalism. There is also a positive and highly significant relationship between included angle of curvature and climbing. Species that perform

high proportions of climbing behaviors have phalanges that are more curved than species that perform lower degrees of these arboreal locomotor activities. In addition, smaller primates generally perform higher proportions of climbing behavior, which includes vertical climbing and pronograde clambering on small branches.

TABLE 5 ABOUT HERE

The regression coefficients presented in Table 5 are used as predictive models to infer proportions of quadrupedalism and climbing in anthropoids. It is important to test the predictive accuracy of these different models in extant taxa in order to understand their usefulness in inferring locomotor adaptation from fossils. Results of cross-validation using 17 test sets are presented in Table 6. The climbing model based on included angle of curvature and the phalanx size proxy is characterized by the lowest overall mean squared error between predicted and actual proportions of locomotor behavior (Table 6). Both quadrupedalism models have higher overall mean squared error based on the 17 test sets. The humeral torsion model has slightly lower residuals between observed and predicted levels of quadrupedalism compared to the model using olecranon process length and the ulna size proxy. Thus, it is expected that the climbing predictive model will outperform both quadrupedalism regression equations in extant test taxa.

TABLE 6 ABOUT HERE

As shown in Table 7 and Figure 3, the climbing model accurately predicts locomotor behavior in two extant test taxa, *Cercopithecus ascanius* and *Cebus apella*. The point prediction

for climbing in *Cebus apella* only differed by 0.04 from the observed proportion, and the prediction for *Cercopithecus ascanius* matches the mean proportion of climbing observed in natural settings. Both quadrupedalism models predict a high proportion of quadrupedal locomotion in *Cebus apella* and *Cercopithecus ascanius*, but the residuals between predicted and observed behaviors are much higher than those characterizing the climbing model (Table 7; Figs. 4 and 5). Both models under predict *Cebus apella* quadrupedalism and over predict *Cercopithecus ascanius* quadrupedal proportions.

TABLE 7 ABOUT HERE

FIGURE 3 ABOUT HERE

Although not as accurate as the climbing model, each quadrupedalism regression is successful at distinguishing highly quadrupedal extant species from those that perform minimal proportions of quadrupedal locomotion (Fig. 4). When humeral torsion and olecranon process length are used to predict the proportion of quadrupedal locomotion performed by the highly suspensory species, *Pongo abelii*, each trait provides an accurate prediction of 0.06. This species has been observed to perform a relatively low proportion of quadrupedal locomotion (0.08 reported by Thorpe and Crompton [2006]).

TABLE 8 ABOUT HERE

FIGURE 4 ABOUT HERE

Based on the estimated degree of humeral torsion in the KNM-RU 2036AH humerus (92°

reported by Larson [1996]), quadrupedalism is inferred to be the main behavior represented in the *Proconsul heseloni* locomotor profile (Table 8; Fig. 4). The degree of phalangeal curvature in the KNM-RU 2036AC phalanx indicates that climbing is also a significant component of the locomotor behavior of this species (Table 8; Fig. 3). The quadrupedalism and climbing models predict that the overwhelming majority of *Proconsul heseloni* locomotion consisted of these two behaviors. The predicted proportion of *Proconsul* quadrupedalism is similar to those predicted for *Lophocebus albigena* and *Macaca fascicularis*. The inferred proportion of climbing locomotion characterizing *Proconsul* is similar to those predicted for *Lophocebus albigena* and *Colobus guereza*. Thus, the estimated degree of humeral torsion and the degree of phalangeal curvature measured in *Proconsul heseloni* most closely resemble arboreal cercopithecoids such as *Lophocebus albigena*.

FIGURE 5 ABOUT HERE

Curvature values and the size proxy measured in the *Pliopithecus vindobonensis* proximal phalanges predict a slightly lower proportion of vertical climbing and clambering as that reported for *Proconsul heseloni* (Table 8; Fig. 3). This prediction is similar to those based on proximal phalangeal curvature values in *Presbytis melalophos*, *Cebus apella*, and *Lophocebus albigena*. Our measurement of humeral torsion in *Pliopithecus* is comparable to that reported by Larson (1996) and falls into the range of values reported for suspensory hominoids and atelids. This trait predicts that *Pliopithecus* performed a relatively low degree of quadrupedalism compared to *Proconsul heseloni* (Table 8; Fig. 4). *Presbytis melalophos, Trachypithecus obscurus*, *Cebus apella*, and *Ateles geoffroyi* provide similar predictions based on humeral torsion. In contrast,

the relatively long olecranon process measured in *Pliopithecus vindobonensis* indicates that this species was adapted to perform a high degree of quadrupedalism as predicted in arboreal cercopithecines such as *Lophocebus albigena*, *Macaca fascicularis*, and *Cercopithecus ascanius* (Table 8; Fig. 5).

Discussion

As described in the results section, a posteriorly oriented humeral head characterizes anthropoids that perform a relatively high proportion of quadrupedalism. The low degree of humeral torsion in these species is the consequence of several skeletal adaptations to quadrupedalism in the thorax and shoulder girdle. Cercopithecoids and platyrrhines that perform a high proportion of quadrupedalism have a narrower and deeper thorax and a more laterally positioned scapula than hominoids and *Ateles* (Erikson, 1963; Sarmiento, 1985; Chan, 2007). A laterally positioned scapula is part of a functional complex that is adaptive for the constricted forelimb movements in a parasagittal plane that characterize quadrupedal locomotion (Larson and Stern, 1989). The ulnar olecranon process is shown to increase in length with increased quadrupedal locomotion. This skeletal feature is the insertion site for the triceps brachii muscle, which is the main elbow extensor. Highly suspensory anthropoids have been shown to have relatively shorter olecranon processes than highly quadrupedal species (e.g., Harrison, 1989; Drapeau, 2004; Rein, 2010). It has been suggested that the relative decrease in olecranon process length in suspensory species is an adaptation to greater forearm extension velocity over long arcs (Stern, 1974; Drapeau, 2004).

When size is incorporated into the model, phalangeal curvature has a high positive

correspondence with climbing behavior (i.e., pronograde clambering and vertical climbing). In addition to corresponding with suspension, this character has been linked to reducing strains when climbing on small supports in which joint reaction forces are oriented dorsally (Richmond, 2007). The results of the present study support this biomechanical model. Similar to humeral torsion, the degree of phalangeal curvature has been suggested to change during an individual's development corresponding with shifts in locomotor behavior during ontogeny (Richmond, 1998).

The conventional least-squares regression (based on a star phylogeny) is the best fit for the three correlations examined in this study. Based on the definition of quadrupedalism employed in this study (excluding knuckle-walking and fist-walking), highly quadrupedal taxa across different anthropoid clades are characterized by similarly low degrees of humeral torsion. Cercopithecoids and the highly quadrupedal atelid, *Alouatta seniculus*, have posteriorly oriented humeral heads compared to hominoids and suspensory non-hominoids. Since this relationship holds across anthropoid clades, the nonphylogenetic model is the best fit for the data. A similar lack of covariation among closely related species in the correlations between olecranon process length and quadrupedalism and phalangeal curvature and climbing makes nonphylogenetic regressions the models of best-fit in these cases as well.

The high correspondence and lack of phylogenetic signal between each forelimb trait and quadrupedalism is the result of the quadrupedalism definition employed in this study. The inclusion of knuckle-walking into this category, which makes up the overwhelming majority of African ape locomotion, would have led to the inclusion of highly quadrupedal species with medially oriented humeral heads and relatively short olecranon processes. Models based on the inclusion of knuckle-walking into the quadrupedalism category would not provide predictions

that are as accurate as the ones employed in the current study.

The climbing model is characterized by the lowest overall mean squared error and most accurate predictions in extant test taxa. The relatively higher accuracy in the climbing model compared to the quadrupedalism models could be the result of the skeletal trait used to make each prediction. The climbing model is based on phalangeal morphology, whereas the two quadrupedalism models are based on more proximal limb segments. The greater correspondence between the manus and locomotor behavior might be in part due to the direct interaction between the substrate and these aspects of the limbs during locomotion.

Although the quadrupedalism models are not as accurate as the climbing model, they are useful in discriminating between highly quadrupedal species and those that perform minimal degrees of quadrupedalism. Both humeral torsion and olecranon process length + ulna size proxy models accurately predict the minimal proportion of quadrupedalism observed in the highly suspensory *Pongo abelii*. Thus, even though these predictive equations are characterized by higher residuals between point predictions and observed proportions, they appear to reliably indicate whether or not a species performs a significant degree of quadrupedal locomotion.

Based on phalangeal curvature, *Proconsul heseloni* is inferred to perform a significant proportion of climbing behavior similar to that predicted for *Lophocebus albigena*. *Pliopithecus vindobonensis* is characterized by a predicted proportion of climbing behavior that is significant but slightly lower than that of *Proconsul*. Even though the proximodistal portion of the olecranon process and proximal humerus are missing in *Proconsul heseloni*, Larson (1996) was able to predict a low degree of humeral torsion (92°) in the KNM-RU 2036 humerus using the position of the bicipital sulcus. Based on this degree of torsion, *Proconsul heseloni* is predicted to mainly employ quadrupedalism during locomotion. In contrast, the relatively high degree of

humeral torsion measured in *Pliopithecus vindobonensis* predicts that this species performed a much lower proportion of quadrupedalism compared to *Proconsul*. However, olecranon process length predicts that *Pliopithecus* would have performed a high proportion of quadrupedalism. The clear contradiction between the humeral torsion and the olecranon process results indicate the limitations of inferring extinct catarrhine locomotor behavior based on extant primate morphology when no extant species has the same combination of traits characterizing the extinct taxon. However, some extant taxa with medially-oriented humeral heads, such as *Ateles geoffroyi*, do combine a significant proportion of quadrupedal locomotion with suspensory and climbing activities. Thus, we suggest that *Pliopithecus vindobonensis* combined pronograde quadrupedalism with a range of antipronograde behaviors including suspension and vertical climbing. This conclusion is similar to Rose (1994), who described the *Pliopithecus* postcranial remains as evidence for the importance of both quadrupedalism and antipronograde behaviors in the locomotor profile of this taxon.

Proconsul heseloni and *Pliopithecus vindobonensis* are two of the best-studied Miocene catarrhines. The models presented in the current study suggest that *Pliopithecus vindobonensis* was adapted to perform significant proportions of quadrupedalism and climbing. However, this species most likely performed a lower degree of quadrupedalism compared to *Proconsul heseloni* and was adapted for a wide range of behaviors that require further investigation. This study confirms previous assertions that *Proconsul heseloni* engaged mainly in above branch arboreal quadrupedalism and was adapted for powerful grasping during climbing (Corruccini et al., 1975; Morbeck, 1975; Rose, 1983, 1993b; Walker and Pickford, 1983; Begun et al., 1994; Ward, 1998; Dunsworth, 2006). This species was a member of the diverse catarrhine group known as the proconsuloids, which were precursors of hominoids that inhabited the tropical

forests and woodlands of Africa during the early Miocene before cercopithecoids and early hominoids became the dominant taxa in the region (Harrison, 2010). Perhaps the inferred locomotor profile of *Proconsul heseloni* provides a model for the ancestral pattern of locomotor behavior from which later hominoids evolved beginning in the Miocene.

Conclusions

Humeral torsion and olecranon process length have been shown to correlate strongly with quadrupedal locomotion in anthropoids. The humeral head is oriented more posteriorly and the olecranon process is relatively long in highly quadrupedal cercopithecoids and platyrrhines. In addition, species that perform a high proportion of climbing have more curved phalanges than those that do not. Since these functional relationships exist across distantly related taxa, there is an absence of phylogenetic signal in the correspondence between these traits and behaviors. When size is taken into account, phalangeal curvature accurately predicts climbing behavior across anthropoid taxa. Both quadrupedalism models are less accurate than the climbing model, but they are able to discriminate among highly quadrupedal species and those that perform minimal amounts of quadrupedalism in extant anthropoids. The climbing model and quadrupedalism model based on humeral torsion confirm previous assessments of locomotor behavior in *Proconsul heseloni* and predict that this species would be characterized by a high proportion of quadrupedal locomotion and a significant amount of climbing behavior. The combination of a high degree of humeral torsion and long olecranon process in *Pliopithecus vindobonensis* suggests that this species combined quadrupedalism with a range of antipronograde behaviors during locomotion.

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Figure legends

Fig. 1. Phylogenetic tree and branch lengths for 17 species used in construction of prediction models. Divergence dates between taxa are in millions of years and based on molecular studies including Tosi et al. (2003, 2005), Raaum et al. (2005), Opazo et al. (2006), Steiper and Young (2006), and Sterner et al. (2006).

Fig. 2. Landmarks of measurements taken on humerus, ulna, and third proximal phalanx. Images include: a, human left humerus in anterior view; b, human left ulna in lateral view; c, human left phalanx in lateral view. Measurements based on these landmarks are described in the text.

Fig. 3. Point predictions and 95% confidence intervals for climbing behavior in *Cebus apella*, *Cercopithecus ascanius*, *Proconsul heseloni*, and *Pliopithecus vindobonensis*.

Fig. 4. Point predictions and 95% confidence intervals for quadrupedalism based on humeral torsion in *Cebus apella*, *Cercopithecus ascanius*, *Pongo abelii*, *Proconsul heseloni*, and *Pliopithecus vindobonensis*.

Fig. 5. Point predictions and 95% confidence intervals for quadrupedalism based on olecranon process length in *Cebus apella*, *Cercopithecus ascanius*, *Pongo abelii*, and *Pliopithecus vindobonensis*.

Table 1

Sample and variables used to build predictive models[a]

Taxon	HT			OL			IA		
	n	**Mean**	**SD**	***n***	**Mean**	**SD**	***n***	**Mean**	**SD**
Alouatta seniculus	19	96.4	8.9	19	17.5	2.3	15	36.9	6.3
Ateles geoffroyi	9	105.8	11.0	12	15.0	0.6	7	50.8	8.3
Cercopithecus mitis	20	95.5	8.5	20	15.1	2.2	21	31.0	7.6
Chlorocebus aethiops	20	94.6	8.8	20	13.6	1.7	20	24.2	7.7
Colobus guereza	20	98.3	7.9	20	17.0	1.9	20	30.1	5.7
Gorilla gorilla	20	133.7	12.2	20	28.6	4.5	20	41.1	5.3
Homo sapiens	20	158.1	9.4	20	20.4	1.9	20	29.1	4.3
Hylobates lar	20	115.3	14.3	20	9.5	0.9	20	45.5	4.8
Lagothrix lagothricha	17	100.8	7.2	17	15.7	1.3	13	53.3	5.0
Lophocebus albigena	18	93.1	9.1	13	16.6	1.7	6	29.5	10.1
Macaca fascicularis	10	94.3	10.9	10	15.7	0.9	10	16.2	6.6
Pan troglodytes	20	132.9	9.6	20	23.4	2.3	21	38.4	5.3
Papio anubis	20	90.1	4.7	20	27.5	3.0	19	14.7	5.0
Pongo pygmaeus	10	112.9	10.9	10	17.6	1.5	11	64.2	13.2
Presbytis melalophos	10	97.8	6.6	11	13.9	1.4	11	25.4	4.8
Procolobus badius	20	96.1	7.3	20	16.2	1.4	14	46.1	9.1
Trachypithecus obscurus	18	102.6	8.1	20	13.9	1.2	20	33.3	7.3

[a] All species, except *Homo sapiens*, are wild-shot. Values for HT and IA are in degrees. Values for OL are in mm. Abbreviations: HT, humeral torsion; OL, olecranon process length; IA, included angle of curvature.

Table 2

Size variables used in this study[a]

Taxon	Ulna SS			Phalanx SS		
	n	**Mean**	**SD**	***n***	**Mean**	**SD**
Alouatta seniculus	19	9.0	0.8	15	3.4	0.6
Ateles geoffroyi	12	9.3	0.4	7	3.5	0.2
Cercopithecus mitis	20	8.3	0.9	21	2.7	0.4
Chlorocebus aethiops	20	7.6	1.0	20	2.4	0.3
Colobus guereza	20	9.6	1.1	20	3.4	0.3
Gorilla gorilla	20	23.8	3.2	20	9.1	0.9
Homo sapiens	20	17.4	1.3	20	6.8	0.6
Hylobates lar	20	8.3	0.5	20	3.8	0.4
Lagothrix lagothricha	17	9.0	0.7	13	3.2	0.6
Lophocebus albigena	13	9.3	1.1	6	3.4	0.3
Macaca fascicularis	10	8.0	0.3	10	2.7	0.2
Pan troglodytes	20	17.0	1.6	21	8.0	0.5
Papio anubis	20	14.0	1.3	19	4.4	0.6
Pongo pygmaeus	10	16.4	1.2	11	6.5	0.8
Presbytis melalophos	11	8.6	0.6	11	3.5	0.2
Procolobus badius	20	9.8	0.9	14	3.7	0.3
Trachypithecus obscurus	20	8.8	0.5	20	3.2	0.2

[a] All values are in mm. ULNA SS, ulna skeletal size surrogate based on five measurements employed by Drapeau (2004). Measurements include include proximodistal height of the trochlear notch, maximum depth of the trochlea, proximodistal diameter of radial notch, anteroposterior length of the coronoid process, anteroposterior diameter at the midshaft; Phalanx SS, proximal third phalanx skeletal size surrogate based on anteroposterior midshaft diameter.

Table 3

Mean proportions of species locomotion used to build predictive models[a]

Taxon	QUAD	CLIMB	Citations[b]
Alouatta seniculus	0.51	0.29	1,2,3
Ateles geoffroyi	0.33	0.21	4,5,6
Cercopithecus mitis	0.54	0.35	7
Chlorocebus aethiops	0.54	0.30	8
Colobus guereza	0.38	0.26	7,8
Gorilla gorilla[c]	0.02	0.04	9,10
Homo sapiens	0.00	0.00	NA
Hylobates lar	0.00	0.34	11
Lagothrix lagothricha	0.29	0.43	12,13
Lophocebus albigena	0.42	0.32	7,14
Macaca fascicularis	0.68	0.23	15, 16
Pan troglodytes[c]	0.04	0.06	17,10
Papio anubis	0.99	0.01	18
Pongo pygmaeus	0.12	0.26	19
Presbytis melalophos	0.24	0.14	20
Procolobus badius	0.35	0.26	7,14,21
Trachypithecus obscurus	0.58	0.12	20

[a] Abbreviations: QUAD, proportions of quadrupedalism; CLIMB, proportions of climbing.

[b] Cited sources: 1, Schön Ybarra (1984); 2, Youlatos (1998a); 3, Fleagle and Mittermeier (1980); 4, Mittermeier (1978); 5, Bergeson (1996); 6, Fontaine (1990); 7, Gebo and Chapman (1995a); 8, Rose (1979); 9, Remis (1994); 10, Carlson (2005); 11, Fleagle (1980); 12, Cant et al. (2001); 13, Defler (1999); 14, Aronsen (2004); 15, Cant (1988); 16, Crockett and Wilson (1980); 17, Doran and Hunt (1994); 18, Hunt (1989); 19, Cant (1987); 20, Fleagle (1977); 21, McGraw (1996).

[c] Proportions of knuckle-walking quadrupedalism were not included in this analysis since we were interested in building predictive models for "monkeylike" quadrupedal behavior. If knuckle-walking proportions were included, accurate predictions could not be made regarding palmigrade or digitigrade quadrupedalism.

Table 4

Results of regression analysis[a]

Behavior	Trait	Model	lnML	AIC_c	MSE	SEE
QUAD	HT	OLS	-29.8	71.0	2.2	1.5
		GLS	-37.7	86.8	5.6	2.4
		GLS Pagel's λ	-29.8	75.1	2.2	1.5
		GLS OU	-29.5	74.4	2.1	1.5
QUAD	OL	OLS	-28.4	68.1	2.0	1.4
		GLS	-32.4	76.1	3.2	1.8
		GLS Pagel's λ	-28.4	72.2	2.0	1.4
		GLS OU	-28.4	72.2	2.0	1.4
CLIMB	IA	OLS	-15.4	42.2	0.4	0.7
		GLS	-21.1	53.6	0.9	0.9
		GLS Pagel's λ	-15.4	46.3	0.4	0.7
		GLS OU	-15.3	46.1	0.4	0.7

[a] Regressions with $\log_{10}$OL and $\log_{10}$IA also include a $\log_{10}$SS (size surrogate) as an additional independent variable. Results are shown under the ordinary least-squares model (OLS), generalized least-squares model (GLS), and GLS using Pagel's lambda and OU transformations. Abbreviations: HT, humeral torison; OL, olecranon process length; IA; included angle; OU, Ornstein-Uhlenbeck; lnML, natural logarithm maximum likelihood; AIC_c, Akaike information criterion for small sample size; MSE, mean squared error; SEE, standard error of the estimate.

Table 5

Coefficients of the regression equations for the best-fit models[a]

Behavior	Variable	Coef	SE	*T*	df	p
QUAD	log_{10}HT	-27.3	5.5	-4.9	15	< 0.001
	y intercept	54.5	11.1	4.9	15	< 0.001
QUAD	log_{10}SS	-21.6	4.0	-5.4	14	< 0.001
	log_{10}OL	25.9	5.2	5.1	14	< 0.001
	y intercept	-10.5	3.9	-2.7	14	< 0.05
CLIMB	log_{10}SS	-6.1	1.0	-5.9	14	< 0.0001
	log_{10}IA	4.5	1.0	4.4	14	< 0.001
	y intercept	-4.7	1.5	-3.2	14	< 0.01

[a] Abbreviations: Coef, coefficient; HT, humeral torsion; SS, skeletal size surrogate; OL, olecranon process length; IA, included angle of curvature.

Table 6

Results of cross-validation analysis for models of best-fit[a]

Behavior	Trait	Overall MSE
QUAD	HT	2.6
QUAD	OL + SS	3.2
CLIMB	IA + SS	0.6

[a] Abbreviations: MSE, mean squared error; HT, humeral torsion; OL, olecranon process length; SS, skeletal size surrogate; IA, included angle of curvature

Table 7

Predictions of quadrupedalism and climbing proportions in two test taxa[a]

Taxon	Beh	Traits	Prediction	CI	Obs	Res	Ref[b]
Cebus apella	QUAD	OL + SS	0.37	0.14-0.66	0.54	-0.17	1,2,3
Cebus apella	QUAD	HT	0.31	0.17-0.49	0.54	-0.23	1,2,3
Cebus apella	CLIMB	IA + SS	0.20	0.11-0.33	0.16	0.04	1,2,3
Cercopithecus ascanius	QUAD	OL + SS	0.59	0.33-0.80	0.37	0.22	4,5
Cercopithecus ascanius	QUAD	HT	0.54	0.33-0.74	0.37	0.17	4,5
Cercopithecus ascanius	CLIMB	IA + SS	0.36	0.24-0.50	0.36	0.00	4,5

[a] Abbreviations: QUAD, proportion quadrupedalism; CLIMB, proportion climbing; OL, olecranon process length; SS, skeletal size surrogate; HT, humeral torsion; IA, included angle of curvature; CI, 95% confidence interval; Obs, observed proportions of locomotion; Res, residuals between observed and predicted proportions of behavior.

[b] Cited sources: 1, Fleagle and Mittermeier (1980); 2, Youlatos (1998b); 3, Wright (2007); 4, Gebo and Chapman (1995a); 5, Aronsen (2004).

Table 8

Prediction of locomotion in *Proconsul heseloni* and *Pliopithecus vindobonensis*[a]

Specimen[b]	Beh	Traits	Trait Value	Prediction	CI
Proconsul heseloni	QUAD	HT[c]	92.0	0.68	0.43-0.85
Proconsul heseloni	CLIMB	IA + SS	33.5 + 3.9	0.18	0.13-0.24
Pliopithecus vindobonensis	QUAD	OL + SS	17.7 + 9.8	0.63	0.41-0.82
Pliopithecus vindobonensis	QUAD	HT	114.1	0.14	0.06-0.28
Pliopithecus vindobonensis	CLIMB	IA + SS	36.8 + 4.7	0.14	0.10-0.20

[a]Abbreviations: QUAD, proportion quadrupedalism; CLIMB, proportion climbing; HT, humeral torsion; IA, included angle; OL, olecranon process length; SS, ulna size surrogate; CI, confidence interval.

[b] *Proconsul heseloni* specimens: humerus, KNM-RU 2036AH; proximal phalanx, KNM-RU 2036AC. *Pliopithecus vindobonensis* specimens: one complete humerus (Individual II located in Naturhistorische Museum Wien); two complete ulnae (Individual I located in Naturhistorische Museum Basel, Individual II located in Naturhistorische Museum Wien); left fourth manual proximal phalanx (Individual III located in Naturhistorische Museum Basel).

[c] Humeral torsion value based on estimate from Larson (1996).